

CLADISTIC ANALYSIS OF THE SPECIES OF THE TRAPDOOR SPIDER GENUS *ALIATYPUS* (ARANEAE, ANTRODIAETIDAE)

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ABSTRACT. A cladistic analysis of the 11 species of the antrodiaetid trapdoor spider genus *Aliatypus* generally supports the phylogeny proposed by Coyle (1974) but resolves the polytomy of the four *erebus* group species and suggests that *A. thompsoni* is the sister of the five *californicus* group species.

So many advances in phylogenetic analysis have been made since I proposed the first phylogeny for the Californian trapdoor spider genus *Aliatypus* (Coyle 1974) that I believe it is now appropriate to test that phylogeny with a more rigorous cladistic analysis. Moreover, I have discovered several phylogenetically useful morphological and behavioral characters not used in that first analysis.

Relationships of *Aliatypus*.—Coyle (1971, 1974) believed that the monophyly of the family Antrodiaetidae was arguable and even suggested that the mecicobothriids, rather than *Antrodiaetus* plus *Atypoides*, might be the sister group of *Aliatypus*. Five putative synapomorphies have been proposed to support the hypothesis that the family Antrodiaetidae (composed of *Antrodiaetus*, *Atypoides*, and *Aliatypus*) is monophyletic: 1) an inner conductor sclerite (Coyle 1971; Eskov & Zonshtein 1990), 2) absence of teeth on the median tarsal claw (Raven 1985; Goloboff 1993), 3) fovea a non-transverse or longitudinal pit or absent (Raven 1985; Goloboff 1993), 4) posterior lateral spinnerets (PLS) with three articles (Eskov & Zonshtein 1990), and 5) rastellum (Goloboff 1993). Synapomorphy 4 must be rejected because most atypids, which are generally held to be the sister group of the antrodiaetids (Raven 1985; Coddington & Levi 1991; Goloboff 1993), have three PLS articles, and those atypid species with four articles as adults have three in an early instar (Schwendinger 1990). The other four putative synapomorphies appear in other families as well; character states 2 and 5 are each found in several other families, state 3 may also occur in the mecicobothriids and some diplurids, and state 1 is found in some mecicobothriid species. Therefore, although all important studies of my-

galomorph family relationships within the last decade agree that the antrodiaetids are monophyletic, the few proposed synapomorphies are all homoplasies. Another possible antrodiaetid autapomorphy is the presence in all three genera of a single spigot on each PLS of the first instar spiderling (Bond 1994; Coyle & Icenogle 1994; Coyle pers. obs.). Yoshikura (1958) remarked that there are no spigots on first instar *Atypus karschi* spiderlings, but further study of this character in atypids and other taxa is required to assess its phylogenetic value.

The current consensus is that *Antrodiaetus* plus *Atypoides* is the sister group of *Aliatypus* (Raven 1985; Eskov & Zonshtein 1990; Goloboff 1993). The monophyly of *Antrodiaetus* and *Atypoides* is supported by the following three synapomorphies: 1) fovea longitudinal; 2) slight or pronounced anterodorsal process on male chelicerae; 3) inner conductor sclerite strongly developed, surrounds embolus, and its tip distinctly separate from tip of outer conductor sclerite. The status of another synapomorphy cited by Raven (1985), the reduction of the anterior lateral spinnerets (ALS), is problematic. The ALS of *Atypoides* species appear to be as well developed as those of atypids; at least some atypids lack ALS spigots while many individuals of *Atypoides riversi* have one ALS spigot (Coyle 1968).

Monophyly of *Aliatypus*.—Whether one uses the atypids alone (Raven 1985; Coddington & Levi 1991; Goloboff 1993) or the atypids plus mecicobothriids (Eskov & Zonshtein 1990) as the outgroup of antrodiaetids, several synapomorphies support the monophyly of *Aliatypus* as defined by Coyle (1974): 1) two rows of cheliceral teeth, one prolateral and one retrolateral; 2) male pedipalp patella elongate; 3) no pseudo-segmen-

tation on male tarsi; 4) trapdoor entrance; and 5) pendulous egg sac which occludes burrow lumen.

CHARACTERS AND METHODS

Although nine of the 18 morphological characters used in this analysis were employed in Coyle's (1974) earlier phylogenetic analysis, some of these have been redefined and quantified. The nine morphological characters used here for the first time were chosen after careful searching through the diagnoses and quantitative character tables in Coyle (1974) for character states which distinguish two or more species from the rest. Twelve characters are either measurements or diagnostically useful ratios derived from measurements and meristic characters. The five behavioral/ecological characters are from Coyle & Icenogle (1994). Characters autapomorphic for single species were not included in the analysis since they provide no information on relationships. MacClade version 3.0 (Maddison & Maddison 1992) was used to analyze character evolution and find the shortest trees.

Character states.—I have used *Antrodiaetus* plus *Atypoides* as the outgroup to determine character state polarities. In the list of characters that follows, the first state mentioned for each character is the plesiomorphic state (exhibited by both *Antrodiaetus* and *Atypoides*), except for characters 21–23 where the polarity is unknown. Every character is treated as unordered except for four of the multistate characters (4, 10, 12, and 14), which were ordered. The other two multistate characters (9 and 13) were not ordered because each of the two derived states is as similar or more similar to the ancestral state than to the other derived state. (If these two characters are ordered, the shortest tree is longer but its form is unchanged.) See Coyle (1974) for definitions of measurement characters and for drawings of many of these character states. CL is carapace length, AMD the transverse diameter of an anterior median eye pupil, PSL the maximum diameter of a posterior sigillum, PSS the distance between the posterior sigilla, CMT the number of microteeth on a chelicera, PTL palpal tibia length, PTT palpal tibia maximum diameter, IFL femur I length, ITL tibia I length, IML metatarsus I length, ITarL tarsus I length, and IVTL tibia IV length.

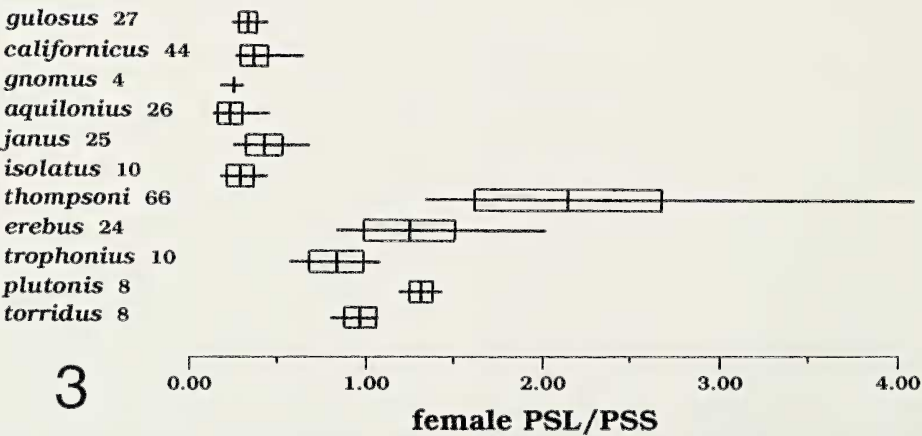
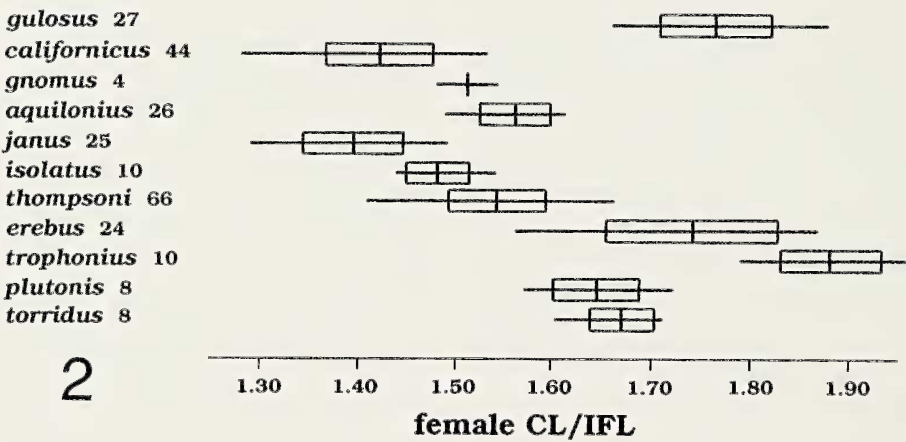
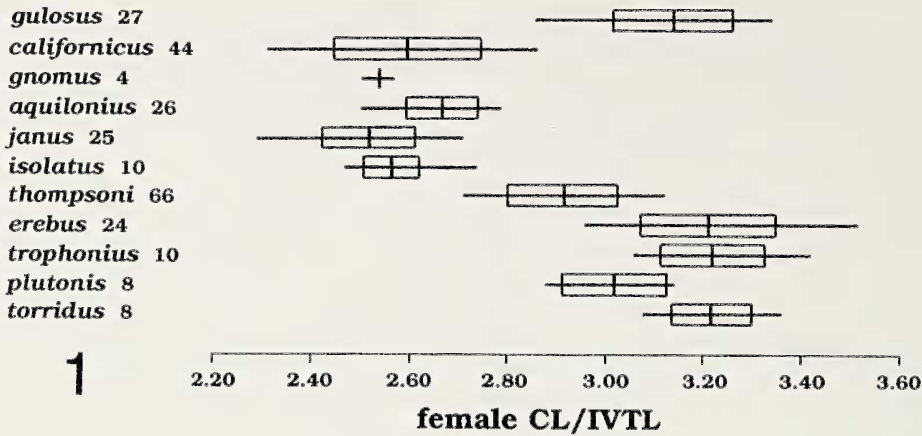
1) Outer conductor sclerite (OCS) of the palpal organ serrate; not serrate. 2) Receptaculum seminis of palpal organ loosely looped; tightly looped.

3) Spermathecal stalks straight; sinuous. 4) Male palpal tibia not expanded distally; expanded distally (mean $PTT/PTL = 0.18-0.27$); greatly expanded distally ($0.39-0.40$). 5) Live in places with cold (snowy) winters; mild (rainy) winters. 6) Outer conductor sclerite (OCS) without keel; keel present. 7) Female tibia IV proportionally long (mean $CL/IVTL = 2.52-2.67$); proportionally short ($2.91-3.22$) (Fig. 1). 8) Female femur I proportionally long (mean $CL/IFL = 1.39-1.56$); proportionally short ($1.64-1.88$) (Fig. 2). 9) Posterior sigilla small and far apart (mean $PSL/PSS = 0.22-0.42$); large and moderately close ($0.82-1.30$); large and very close (2.13) (Fig. 3). 10) Male tibia I proportionally long (mean $CL/ITL = 1.38-1.66$); proportionally short ($1.81-1.85$); proportionally very short ($2.16-2.18$) (Fig. 4). 11) Cheliceral microteeth (CMT) relatively numerous (mean $CL/CMT = 0.32-0.52$); relatively few ($0.88-0.94$). 12) Silk lining of burrow thin; moderately thick; thick. 13) Male metatarsus I of medium length (mean $CL/IML = 1.41-1.70$); proportionally long (1.14); proportionally short ($1.92-1.95$) (Fig. 5). 14) Spermathecal stalks very short relative to bulb diameter; medium length relative to bulb diameter; very long relative to bulb diameter. 15) Spermathecal stalks as wide distally as at base; narrowed distally (tapered). 16) Length of male metatarsus I short relative to tarsus (mean $IML/ITarL = 1.61-1.89$); long relative to tarsus ($2.10-2.14$). 17) Inner conductor sclerite (ICS) without keel; keel present. 18) Door relatively thin and semi-rigid; relatively thick and rigid. 19) Body size large (mean female $CL = 5.7-7.8$); small ($3.8-4.4$). 20) Anterior median eyes proportionally small (mean female $CL/AMD = 39-51$); proportionally large ($28-33$). 21) Door proportionally broad (mean door shape index = $1.42-1.66$); proportionally narrow ($1.18-1.28$) (polarity not assigned because outgroup does not make trapdoors) (Fig. 6). Door shape index = width/height. 22) Usually inhabit gentle slopes; steep slopes (polarity not assigned because outgroup exhibits both states). 23) Distance from base of embolus to tip of conductor (PED) relatively large (mean $CL/PED = 3.7-4.3$); relatively small ($5.1-5.3$) (polarity not assigned because PED not recorded for outgroup).

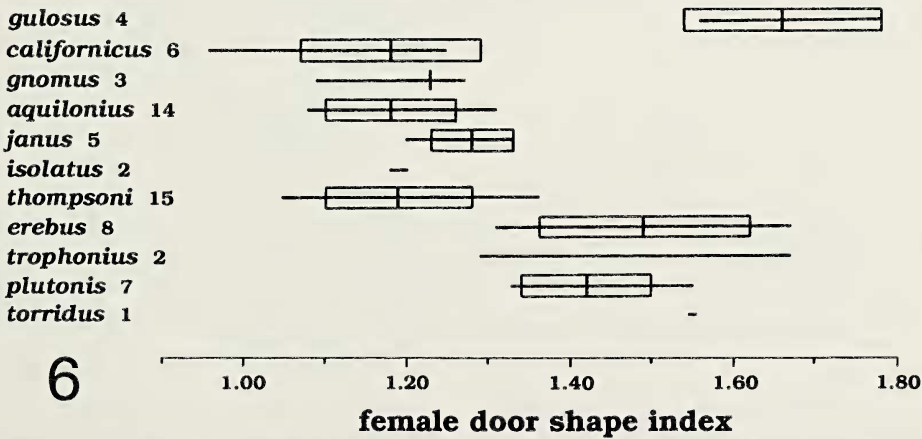
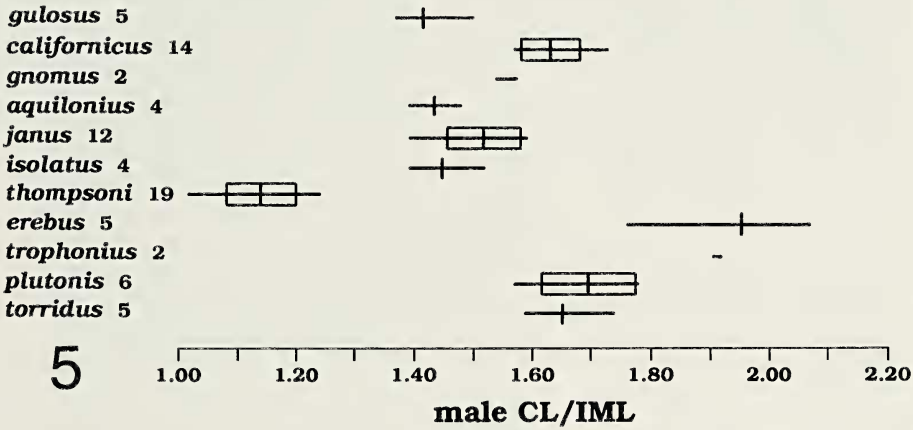
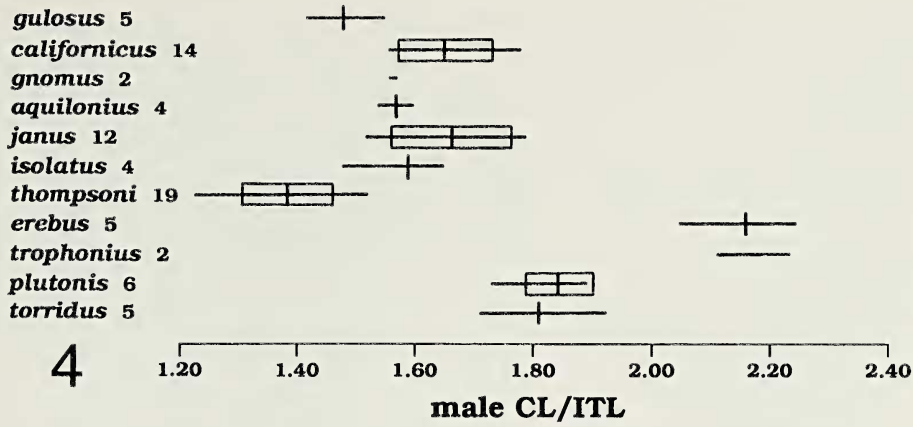
The distribution of these character states among the species of *Aliatypus* is shown in Fig. 7.

RESULTS AND DISCUSSION

The shortest tree (length (TL) = 42, consistency index (CI) = 0.69, retention index (RI) = 0.77)



Figures 1-3.—Diagrams comparing quantitative character values of *Aliatypus* species. Horizontal bar represents the range, vertical bar the mean, and box the standard deviation (if sample size greater than 5). Sample size given next to species name. 1, female CL/IVTL; 2, female CL/IFL; 3, female PSL/PSS.



Figures 4-6.—Diagrams comparing quantitative character values of *Aliatypus* species. Horizontal bar represents the range, vertical bar the mean, and box the standard deviation (if sample size greater than 5). Sample size given next to species name. 4, male CL/ITL; 5, male CL/IML; 6, female door shape index (width/minimum diameter of door).

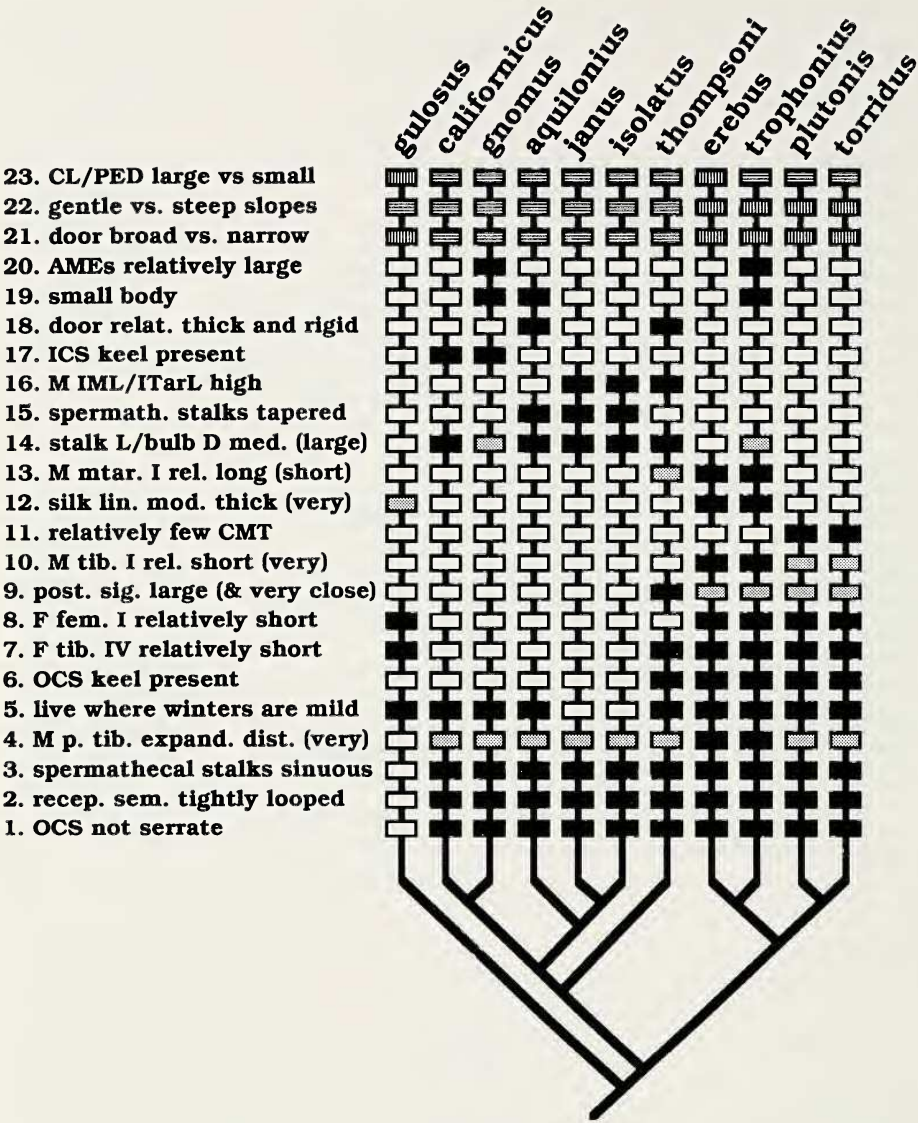


Figure 7.—Most parsimonious cladogram of *Aliatypus* species. Apomorphic states described and designated by black boxes, plesiomorphic states by open boxes. M = male, F = female. For triple-state characters (4, 9, 10, and 12–14), the first described apomorphic state (not in parentheses) is designated by grey (stipples), and the other apomorphic state (in parentheses) by black. For those characters of unknown polarity (21–23), the first state described is designated by vertical lines, the second by horizontal lines.

without polytomies is presented in Fig. 7. That this is the shortest tree was independently confirmed by N. Platnick and P. Goloboff on Hennig86 (Farris 1988) and NONA (Goloboff pers. comm.), respectively. The several next-most parsimonious non-polytomous cladograms (TL = 43, CI = 0.67, RI = 0.75) have the same form as the shortest tree except for various rearrangements within the clade containing *A. thompsoni*

and the five *californicus* group species (*A. californicus*, *A. gnomus*, *A. aquilonius*, *A. janus*, and *A. isolatus*).

Aliatypus gulosus is clearly the most plesiomorphic species, with all ten of the other species forming a sister clade defined by synapomorphies 1–4. The monophyly of the *erebus* group clade (*A. erebus*, *A. trophoni*, *A. plutonis*, and *A. torridus*) is supported by synapomorphies 6–

10 and by shared states of the non-polarized characters 21 and 22. Of these putative synapomorphies, only 9, 10, and 22 are unambiguously synapomorphic when character state changes are optimized (by parsimoniously assigning states to the internal nodes of the tree). The sister group relationship of *A. erebus* and *A. trophonius* is supported by synapomorphies 4, 10, 12, and 13, and that of *A. plutonis* and *A. torridus* by synapomorphy 11.

The monophyly of the *californicus* group is much less strongly supported than that of the *erebus* group. Only character 7 provides a putative synapomorphy (optimization indicates it is a reversal). Within this clade, *A. aquilonius*, *A. janus*, and *A. isolatus* are united by synapomorphy 15, and *A. janus* and *A. isolatus* are united by synapomorphies 5 and 16, synapomorphy 5 (living in habitats with cold winters) being a primitive antrodiaetid trait which evidently reappeared in the immediate common ancestor of these two species. The sister-group relationship of *A. californicus* and *A. gnomus* is supported by synapomorphy 17.

The primary unresolved issue in the original *Aliatypus* phylogeny (Coyle 1974) was the relationship of *A. thompsoni*. The current analysis indicates that *A. thompsoni* is more closely related to the *californicus* group than to the *erebus* group. Synapomorphy 14 (long spermathecal stalks relative to bulb size) and unpolarized character 21 (door shape) support this hypothesis (reversal synapomorphy 8 is ambiguous). Only synapomorphy 6 (synapomorphy 7 is ambiguous) supports the alternate hypothesis that *A. thompsoni* is more closely related to the *erebus* group. Clearly the relatively long male metatarsus I (character 13) is autapomorphic for *A. thompsoni*, as are two character states not used in this analysis: fovea shallow or absent, and the presence of only short macrosetae and strongly adpressed background setae on the tibia and metatarsus of male leg I. I also interpret this species' especially close-spaced posterior sigilla (character 9) to be an autapomorphy, even though similar in size to the proportionally large posterior sigilla of the *erebus* group species.

It is important to point out that changes in the definitions and assumptions for only a few characters would favor the alternative hypothesis that *A. thompsoni* is sister to the *erebus* group. If character 9 is reinterpreted to comprise only two states (posterior sigilla small and far apart vs. large and close) and if character 14 is treated as unordered,

then the two hypotheses (*A. thompsoni* is sister to the *californicus* group, or to the *erebus* group) are equally parsimonious (TL = 41, CI = 0.68, RI = 0.76). If, in addition to these changes, behavioral character 21 (door shape) were unknown, the single shortest resulting tree would place *A. thompsoni* as the sister of the *erebus* group.

The shortest tree (Fig. 7) contains 11 homoplasies (in characters 6–8, 14, 16, 18–20, and 23), four of which involve *A. thompsoni* (apomorphies 6, 7, 16, and 18). The most frequent homoplasy is the evolution of small body size (character 19), which has evidently arisen in three different lineages.

Although I was careful to select only those quantitative characters with marked discontinuities separating clusters of species, the designation of character states in one of these, character 10, is somewhat arbitrary (Fig. 4). Fortunately, alternate character coding which could result from this arbitrariness (assigning *A. thompsoni*, or *A. thompsoni* and *A. gulosus*, to a third derived character state defined as "male tibia I especially long") does not change the form of the shortest tree, but only lengthens it.

In conclusion, this cladistic analysis supports, in general, the original phylogeny (Coyle 1974), which was developed via a semi-cladistic analysis using fewer characters. The new phylogeny is similar to the old except that it resolves the polytomy in the *erebus* group and roots *A. thompsoni* to the stem of the *californicus* group.

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